

The University of Chicago

ON THE MUSCULAR ACTIVITY OF  
THE COLON IN THE DOG

A DISSERTATION SUBMITTED TO THE  
GRADUATE FACULTY IN CANDIDACY FOR  
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PHYSIOLOGY

By  
HAMPDEN CLISBY LAWSON

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ON THE MUSCULAR ACTIVITY OF THE COLON  
IN THE DOG\* (1)

Elliott and Smith in 1904 (2) in a study of the comparative physiology of the colon described the dog's colon as a rather rudimentary organ, as compared with the more complicated large intestine of herbivora. The characteristic motor activity in this animal, according to these observers, was peristalsis, primarily an excretory mechanism. In 1900 Bayliss and Starling (3) had confirmed their "law of the intestine" on the colon in anesthetized dogs, and stated that "the activity of the local mechanism diminishes from the ileocecal valve to the anus, so that under normal circumstances the extrinsic innervation is of more importance than the intrinsic in the emptying of the lower segment of the colon." They further assumed some degree of specialization in the dog's colon because of the slower rhythmicity. Fellner, in 1883 (4) had studied the dog's distal colon in situ and had concluded that this part of the tract has a specialized reciprocal innervation for the circular and longitudinal coats.

Cannon's roentgenologic studies of the cat's colon (5) and Zondek's direct observations of colon motility in the

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\*The observations recorded here have been published under joint authorship with R. D. Templeton in a series of papers to which reference is made.

rabbit through a celluloid Bauchfenster (6) have been important contributions to an understanding of the spontaneous motility of the colon. Most of the more recent observations on the human have been made by Cannon's method, in the course of clinical studies (7), (8), (9), (10). Peiper (11), Ganter and Stattmüller (12) and Weitz and Vollers (13) have made observations on the human by introducing balloons into the lumen of the colon, either by anus or through colostomies or cecostomies.

Little has been added, however, to the observations of Elliott and Smith on the motor activity of the colon in the dog, although the findings of Fellner and of Bayliss and Starling deserve further consideration. This is in spite of the fact that a great deal of pharmacological work has been done on the dog's colon, usually with single balloons inserted by way of cecostomies (14), (15), (16). The extrinsic innervation of the colon is not yet completely solved (17), (18).

For the purpose of investigating further the spontaneous motility of the colon in the dog, balloons were inserted into the proximal colon through a cecostomy, and into the distal colon by anus. In this way as many as six balloons were placed in recording position in the colon, filled with air, and the pressure-volume changes recorded by means of water manometers. The balloons were tied together in tandem so that their relative positions were unaltered during the course of the tracing (19). In this way records were made simultaneously

of pressure changes in all parts of the colon. The dogs used in the study were trained to lie quietly without anesthesia while the tracing was being taken. Diet and the conditions of the experiment, such as degree of inflation and position of the balloons, were adequately controlled.

Balloon tracings of the colon showed, in addition to periodic changes in tone, two types of contractions. The more rapid, smaller contractions appeared as small peaks surmounting much slower, higher contractions. Fellner had observed similar contractions in the dog's distal colon (4). De Zilwa (20) in 1901, stated that tracings of the same sort were obtained from the retractor penis due to a type of summation. This smooth muscle, according to him, underwent contraction in small bundles of fibres, more of which being in a state of contraction at a given time produced the "summated" contraction. Magnus, in 1904 (21), made similar observations on isolated strips of intestine, stating that not all bundles of fibres underwent contraction at the same time. As more and more bundles fell into the contraction, relaxation of the bundles not keeping pace, the tone rise was produced. Cowie and Lashmet in 1929 (22) suggested the terminology "primary contraction" and "secondary contraction" for these contractions. In the dog's colon we found that sometimes the smaller waves were augmented without augmentation of the larger, and in some cases, the larger waves apparently were prevented from forming. In tracing pressure waves over the series of balloons, it was



observed that frequently the larger waves on the lower balloons showed fewer superimposed peaks than those on the upper balloons. This suggested the possibility that the delay in the appearance of the large contraction on the lower balloons might be the result of inhibition of one or more of the components of the wave. Such delay would result in the propagation of a pressure wave in the direction of the delay. Alvarez (23) has proposed that propagated or wave-like contractions in the gastro-intestinal tract are the result of gradients in rhythmicity. Pending further investigation of the relationships between the larger and the smaller, superimposed contractions, we have termed the smaller contractions type I, and the larger, on which they are superimposed, type II.

The difference in the activity of the proximal and the distal colon in the dog is as marked as the statements of Bayliss and Starling (3) would indicate. The proximal colon is periodic in its activity, with high tone changes, and a preponderance of wave-like contractions. These are both peristaltic, as Elliott and Smith (2) observed, and antiperistaltic. Antiperistalsis, according to these observers, was not found in the dog's proximal colon. Zondek, however, in 1921 (6), described haustral segmentation as seen through his Bauchfenster, as antiperistalsis and peristalsis alternating in irregular fashion. Since in the proximal colon of the dog we observed a similar alternation, it is possible that this term should be applied, if Zondek's definition be accepted. How-



ever, the peristaltic phase of a period of proximal activity, which usually occurred during the first half of the period, frequently included waves which could be traced well into the distal colon without interruption. Since there are no haustrae in the dog's colon, and since the term haustral segmentation implies activity localized to small segments, we have not adopted the term here.

Following the peristaltic phase of the proximal period, the entire colon goes into a period of activity in which it is impossible to trace pressure waves from one balloon to another. During this phase, frequently contractions appear and disappear on all six balloons simultaneously, as though the entire colon were contracting and relaxing as a unit. We have applied to this type of activity the non-committal term "rhythmic pulsations." This type of activity is characteristic of the distal colon, peristalsis being usually confined to the proximal colon. During the peristaltic phase of the proximal colon, distal colon activity, and the tone of the distal segment, is depressed. The depression of tone is most marked in the region of the internal anal sphincter, where sometimes the manometers record negative pressure. As soon as the waves of propagated activity begin to appear on balloons lying in the region of the splenic flexure, all balloons lying distally respond simultaneously with rhythmic pulsations, and the peristaltic activity of the more proximal balloons is either completely depressed, or converted into the distal type of

activity.

Tracings of the entire colon, then, show a reciprocal relationship between peristalsis in the proximal segment, on the one hand, and non-propagated activity in the distal segment, on the other. Bayliss and Starling (3) described inhibition of the entire lower colon during peristalsis in the upper segment, but did not mention depression of peristalsis with resumption of distal activity. Langley and Magnus (24) found an occasional reversal of the "law of the intestine" in the distal colon of the rabbit. Weitz and Vollers (13) observed depression of balloon activity high in the distal colon in man, on inserting and inflating a balloon in the rectum. We have observed, on the dog, that stimulation of the distal colon activity, which we termed rhythmic pulsations, either electrically (faradic currents of moderate strength), or by inserting balloons through the anal sphincters, depressed proximal activity, if the latter was peristaltic in type. We found, further, that these stimulations were most effective if applied in the region of the sphincters. The reciprocal relationship between proximal and distal types of activity was not disturbed after transection of the colon in the region of the splenic flexure.

Taking advantage of this reciprocal relationship between proximal and distal segments, we investigated the disturbance of motility in the colon due to the presence of the recording apparatus. Records were made, for example, of

proximal colon motility with and without balloons in the distal colon. For a time following the insertion and inflation of balloons in the distal colon, the proximal colon was depressed. Usually within one hour there was recovery from the depression. At this time the distal colon had diminished in activity, and began to alternate in periodic activity with the proximal. From this point the proximal tracing was not different from the control tracing, without balloons in the distal segment. We concluded, from this, either that the distal colon, after recovery from the immediate effects of insertion, resumes the activity which it showed before balloons were inserted, or that its activity is so little altered by the presence of balloons that the proximal colon fails to record the difference. Similar comparisons were made of distal tracings before and after inserting and inflating balloons in the proximal segment. Except that the immediate effects of inserting balloons through the cecostomy were less constant, and less striking, we were not able to detect any alteration in distal activity, except temporarily.

With the balloons inflated to recording pressure, which varied from 2 to 10 cm. water with the tone of the segment, the volume of air being kept constant in inflating the balloons, we observed the effect of doubling the volume of the air in the balloons. Such increases in volume would adequately cover errors in inflation due to inaccuracy in reading the manometers, or to variation in the capacity of the balloons. It



was found that such over-inflations in the distal colon produced no change in activity, and in the proximal colon only temporary alteration in the tone and activity. The colon seemed to relax to accommodate the increased volume. In a few cases these moderate over-inflations in the proximal colon were followed by apparent augmentation of activity in the balloons lying above. No such effect was seen in the distal colon.

Peiper (11) obtained similar effects on moderately over-inflating balloons in the distal colon of children. However, the work which has been reported using greater degrees of distention (3), (13), (24), (25), which usually results in activation of the distended segment, shows an effect on adjoining segments also.

A method was devised by which the longitudinal and the circular activity of the distal colon could be recorded separately, after transection of the colon in the region of the splenic flexure, and closing off the distal segment to form a pouch. Longitudinal activity was recorded from movements of a plunger placed in contact with the end of the pouch, while circular activity was recorded by tandem balloons.

The longitudinal periods of activity were found to concur with periods of proximal peristalsis, while the type of activity termed rhythmic pulsations bore a reciprocal relationship to both the distal longitudinal activity and proximal peristalsis. Peristalsis was not seen in the distal segment

except in one case, where the distal segment was made so long as to include most of the colon.

Fellner (4) reported a reciprocal relationship between longitudinal and circular activity in the dog's distal colon, and deduced a reciprocal innervation for the two muscle layers. Exner (26), on the other hand, considered such reciprocity to be a general characteristic of the gastro-intestinal tract, and assumed that the primary factor was mechanical. We found the reciprocity to be not invariable. At the close of high longitudinal activity, the circular tracings frequently showed augmentation, in a manner suggesting the sort of relationship observed by Luderlitz (27) who saw circular activity following, at an appreciable interval, the longitudinal. Trendelenburg (28), and others using his isolated segment technique, have usually observed a reciprocal relationship between individual longitudinal and circular contractions. The fact that this relationship can be altered by changing the pressure within the segment may indicate that the apparent reciprocity is due to some such factors as Exner suggests (29).

We have not, as yet, been able to obtain with this method, longitudinal records from the proximal segment, due to anatomical difficulties. Our findings in the distal colon, however, indicate that the longitudinal activity in this region is an important propulsive mechanism. It is significant, for this view, that distal longitudinal activity runs parallel

with peristalsis, the accepted propulsive activity of the proximal segment, and bears a reciprocal relationship to the stationary contractions, especially in the region of the anal sphincters, which are either retarding or retentive in effect.

The fact that after transecting the colon in the region of the splenic flexure, we found the proximal-distal reciprocity undisturbed in balloon records; and that in such preparations the correlation between the longitudinal activity of the distal segment and proximal peristalsis was definite, indicates that these correlations are either humoral or due to long reflexes. On the other hand, whereas peristalsis originating in the proximal colon frequently traverses the entire colon before transection, in the transected preparations we have not been able to trace peristalsis as a wave of constriction over the interruption in the wall. This may be due to the fact that the distal colon, after colostomy, is not distended with material transported from the proximal, and is thus deprived of a stimulus to constriction which Luderlitz at first considered essential (27), but later proved was not necessary in the small intestine (30).

Gleize (31) from purely anatomical considerations, considers the colon to be rather sharply divided into two distinct parts at the level of the splenic flexure. Distal to this point, there are great irregularities in the thickness of the two muscular coats, such as to suggest a functional difference from the proximal colon. Bayliss and Starling (3)



reached similar conclusions from their study of the behavior of the colon. Our data indicate that transection of the colon in the region of the splenic flexure interrupts the propagation of circular activity more completely than the propagation or correlation of longitudinal activity. This suggests a more complete separation, in this region, of longitudinal and circular activity than has been observed in other portions of the gastro-intestinal tract.

#### SUMMARY

1. Balloon tracings of the dog's colon show two types of contractions, the smaller of which are superimposed on the larger, slower contractions in such manner as to suggest a summation.

2. The characteristic activity of the proximal colon is propagated activity, usually peristaltic in the dog. The characteristic activity of the distal colon is non-propagated activity, which frequently occurs as simultaneous pulsations over long segments.

3. A reciprocal relationship exists between the proximal and the distal type of activity, such that each depresses the other.

4. This property can be made use of in calibrating the error thrown into balloon studies of motility in the colon by the introduction of foreign bodies into the lumen.

5. Transection in the region of the splenic flexure interrupts the propagation of waves of constriction into the

distal colon, but proximal-distal reciprocity is undisturbed.

6. The longitudinal activity of the distal segment, after transection of the colon in the region of the splenic flexure, parallels proximal peristalsis, and bears a reciprocal relationship to circular, non propagated activity.

7. The rhythmic pulsations characteristic of the distal colon are a type of circular activity unassociated with generalized shortening of the segment.

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